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Using molecular phylogenies in island biogeography: it's about time

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Island biogeography aims at inferring the processes that govern the assembly of communities in space and time. Molecular phylogenies can tell us about the timings of island colonisations and diversification, but have rarely been used for the estimation of colonisation, speciation and extinction rates on islands. In this study we illustrate the effects of including phylogenetic information with the Galápagos avifauna. We find that by including colonisation times we obtain much more precise and accurate parameter estimates than if we rely solely on species richness and endemism status. Inclusion of branching times improves estimates even further. As molecular phylogenies become increasingly available, we urge biogeographers to start using more of the information they contain.

A major focus of island biogeography has been to understand the processes of colonisation, extinction and speciation on isolated systems (MacArthur and Wilson 1967, Whittaker et al. 2008). Surprisingly, few studies in the field have attempted to estimate parameters relating to process, and those that did often only used diversity data and/or assumed equilibrium dynamics (Triantis et al. 2015, Lim and Marshall 2017). Very few studies have taken advantage of the temporal information encoded in molecular phylogenies regarding when island species colonised and when species diverged from one another (Ricklefs and Bermingham 2001, Rabosky and Glor 2010, Cornuault et al. 2013). Valente et al. (2015, 2017) sought to address this deficiency by including phylogenetic information on both species' colonisation and branching times while relaxing the strong and biologically questionable assumption that diversity is at equilibrium or at carrying capacity. However, it has been suggested that the temporal information offered by phylogenies may be of limited value or lead to erroneous estimates (Lim and Marshall 2017). The focus of our paper is to use simulations to assess the accuracy of this assertion.

We examine whether incorporating more phylogenetic information has any benefit in terms of the accuracy and precision of estimation of colonisation,



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speciation, and extinction rates. Our case study is the Galápagos avifauna, comprising 25 bird species, i.e. all of the archipelago's native resident terrestrial birds excluding rails and birds of prey. We have information on the timings of colonisation (8) and cladogenesis (17) events (Valente et al. 2015).

We used DAISIE (dynamic assembly of islands through speciation, immigration, and extinction), a stochastic dynamic model applied to a given group of species distributed in a given island system (Valente et al. 2015). The model assumes that after a specified time (usually the origin of an island) species colonize at a specified rate. Once a species has colonized, it may become endemic through anagenetic speciation (island population becomes a new endemic species without lineage splitting), split into new species via cladogenetic speciation and/or go extinct. DAISIE is able to infer rates of these processes from the following data: a) age of the island system; b) endemism status of species; c) time of colonization of each of the insular clades;

d) branching times of speciation events within insular clades that have diversified.

We consider three derived datasets of the Galápagos avifauna in order of increasing phylogenetic information: G1 – includes only a+b; G2 – includes a+b+c; and G3 – includes a+b+c+d (Fig. 1). We fitted DAISIE to each of the datasets to estimate the four parameters of the model (colonisation, extinction, cladogenesis and anagenesis) using maximum likelihood (ML). For the G1 data (no phylogenetic information), the ML optimisation failed to converge on a single parameter set (Supplementary material Appendix 1 Table A1), suggesting a hyperplane in parameter space with identical maximum likelihood values. For G2 and G3, we found a clear ML optimum (Supplementary material Appendix 1 Table A1).

We tested how well the model was able to estimate known parameters given the three different types of data (Fig. 1). We simulated 3000 datasets with the ML parameters of the full dataset (G3) and removed data elements

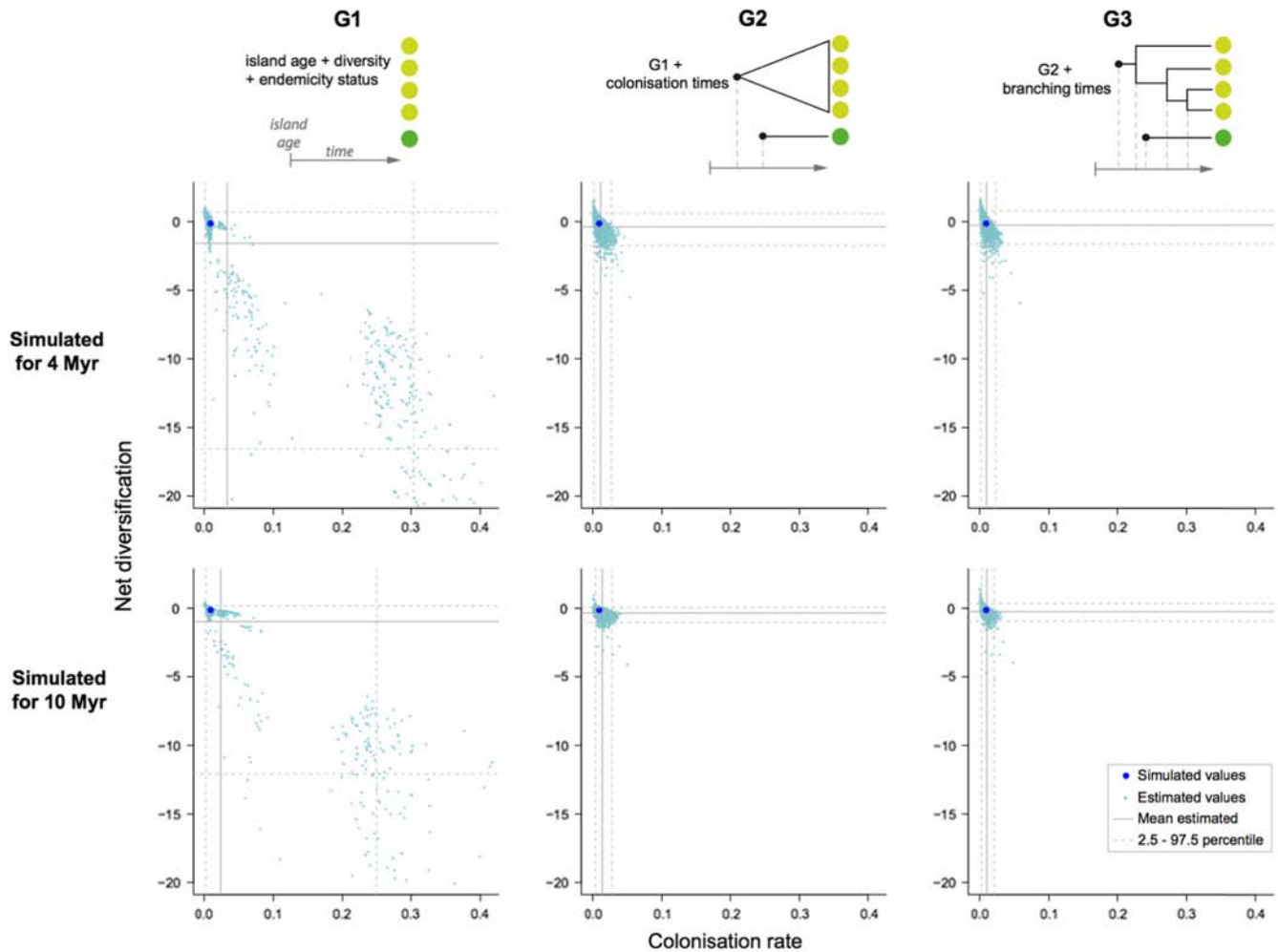


Figure 1. Colonisation rate and net diversification rate (cladogenesis minus extinction) estimates obtained by fitting the DAISIE model to datasets with increasing amount of phylogenetic information. Accuracy and precision under G1 (no phylogenetic data) is low, as revealed by the discrepancies between simulated values and the mean estimates. There is a clear improvement when phylogenetic data is added (G2 and G3). Rates in events per lineage per million years.

to create G1 and G2-type datasets. We ran simulations for 4 million yr (Myr), the age of the Galápagos, producing datasets with a median of 26 species. To assess how dataset size affects estimates, we also ran simulations for 10 Myr, producing larger datasets with a median of 47 species. We then estimated parameters from each of these datasets. Accuracy and precision of parameter estimation was very poor under G1, with two very different clusters of parameters and very wide confidence intervals for all parameters (Fig. 1, Supplementary material Appendix 1 Table A2). In contrast, for the datasets containing phylogenetic information (G2 and G3), we found much narrower confidence intervals (CIs) for all parameters with the exception of anagenesis (Supplementary material Appendix 1 Fig. A1), with G3 outperforming G2. Accuracy and precision were improved when fitting models to larger datasets (simulated for 10 Myr, Fig. 1, Supplementary material Appendix 1 Table A2). Although adding phylogenetic information clearly narrows CIs, for small datasets these can still be quite wide, so this method may not be sufficiently precise for islands with few species. However, with slightly larger datasets, the CIs of G2 and G3 narrow and become biologically informative for all parameters, except anagenesis. The latter may always be difficult to estimate, because cladogenesis plus extinction can produce the same pattern (an anagenetic species).

Our analyses show that the inclusion of phylogenetic data – particularly times of colonisation – greatly improves accuracy and precision for the estimation of key processes of island biota assembly. While the further addition of branching times improves the estimates less in the model of our case study, we expect that the improvement would be more pronounced when speciation is non-constant in time, e.g. under diversity-dependence or when there are fewer colonisations. Note that we do not suggest that phylogenies are always indispensable to estimate parameters – clearly there are cases where phylogenies would be of limited value, for example when dealing with ecological time scales or land bridge islands where colonisation happens frequently (Meiri 2017). However, we argue that studies dealing with remote islands and evolutionary/geological time scales should make more use of temporal information extracted from phylogenetic trees. We now have both the data and methods required to allow phylogenies to mature

from the pages of perspective papers to a highly informative component of the standard analytical toolbox.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.j3073> > (Valente et al. 2018).

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Supplementary material (Appendix ECOG-03503 at < www.ecography.org/appendix/ecog-03503 >). Appendix 1.